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Morphology of the Humerus of *Hapalodectes* (Mammalia, Mesonychia)

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ABSTRACT

A distal humerus of the primitive mesonychian *Hapalodectes* cf. *leptognathus* from the early Eocene of Colorado reveals that *Hapalodectes* was less cursorially derived than were other members of the Mesonychidae such as *Dissacus* and *Mesonyx*. The humerus has a moderately long deltopectoral crest, a relatively wide distal articular surface with a cylindrical capitulum, a relatively broad entepicondyle with an entepicondylar foramen, and a shallow olecranon fossa that lacks a supratrochlear foramen. These skeletal features are associated with terrestrial locomotion but not with cursoriality. This specimen represents some of the first data on the postcranial skeleton of this taxon, data that are relevant both to determination of the sister taxon of Cetacea and for resolving whether or not Mesonychia is paraphyletic.

INTRODUCTION

Hapalodectes is the most diminutive and in many ways the most primitive member of the order Mesonychia (Mesonychidae and Hapalodectidae) (Ting and Li, 1987; Thewissen, 1994; Geisler and O'Leary, 1997; Geisler and Luo, in press; O'Leary, 1998), an aberrant group of extinct Paleogene ungulates from Europe, North America, and Asia. A number of researchers have argued that this order is closely related to cetaceans and that, in particular, an understanding of the primitive postcranial morphology of mesonychians is critical to resolving the question of cetacean origins (Gingerich et al., 1990; Thewissen, 1994; Geisler and Luo, in press; O'Leary, 1998). A particularly close association between *Hapalodectes* and Cetacea has even been suggested (Szalay,

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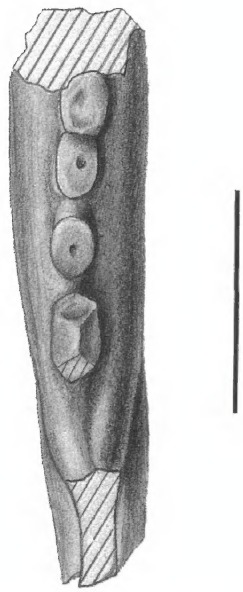


Fig. 1. Right dentary of *Hapalodectes* cf. *leptognathus* (AMNH 17558), M_2 roots and M_3 mesial root and talonid. Scale bar = 10 mm.

1969). *Hapalodectes*, however, has been one of the most difficult mesonychians to place phylogenetically (Geisler and O'Leary, 1997), a problem affecting not only the structure and monophyly of the clade Mesonychia but also broader relationships of the ungulate orders. Recent phylogenetic analyses show that *Hapalodectes* falls either within and at the base of a monophyletic Mesonychia, exclusive of Cetacea (O'Leary, 1998), or outside but close to a clade that includes Cetacea and Mesonychidae (Thewissen, 1994; Geisler and O'Leary, 1997; Geisler and Luo, in press).

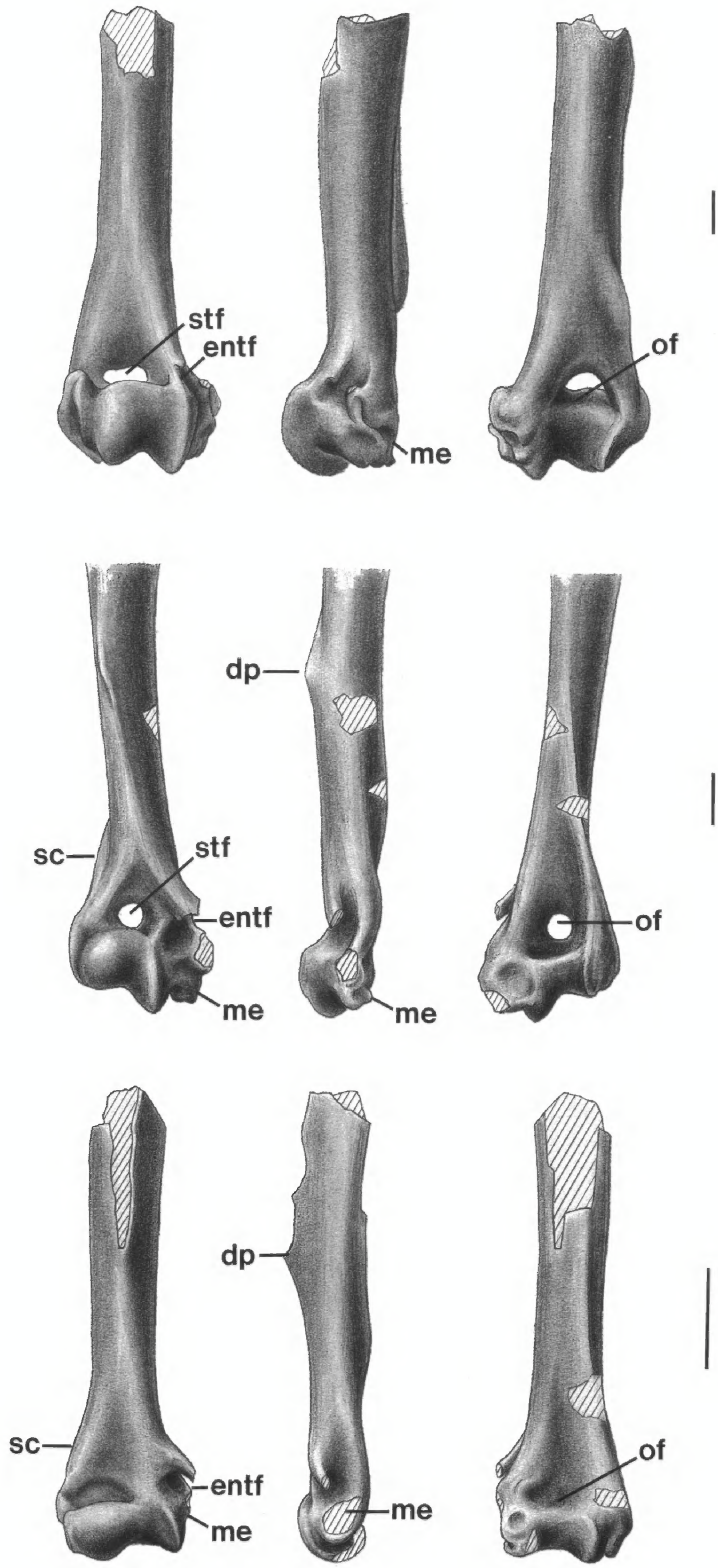
Hapalodectes is known from cranial (Ting and Li, 1987) and dental (Zhou and Gingerich, 1991, and references therein; O'Leary and Rose, 1995a) remains but, until now, nothing of its postcranial anatomy has been figured or described in detail. The only postcranial information on this taxon comes from Rose (1990), who briefly noted a fragmentary specimen from the Willwood Formation, Wyoming. The postcranial skeleton is one of the most important anatomical systems for establishing the relationships of cetaceans to other mammalian orders. This claim stems largely from the hypothesis that cetaceans are closely related to Mesonychia and Artiodactyla (Gingerich et al., 1990; Thewissen and Hussain, 1993; Geisler and Luo, in press; O'Leary, 1998; O'Leary and Geisler, in prep.), two orders diagnosed on a number of postcranial traits. Like artiodactyls, certain mesonychians, such as *Pachyaena* (O'Leary and Rose, 1995b) and *Mesonyx* (Scott, 1888; O'Leary and Rose, 1995b), exhibit features of the postcranial skeleton that are associated with cursoriality. *Dissacus,* which is the most primitive member of the Mesonychidae (Thewissen, 1994; Geisler and O'Leary, 1997; Geisler and Luo, in press; O'Leary, in press; O'Leary and Geisler, in prep.), exhibits some specialized cursorial traits of the humerus (O'Leary and Rose, 1995b) but appears to lack such traits in what is known of the pes, in particular the astragalus, which does not have a grooved trochlea (O'Leary and Geisler, in prep.). Thus it has not yet been established whether or not a cursorially derived skeleton is primitive for Mesonychia. Any information on the postcranial anatomy of *Hapalodectes* is relevant to understanding the primitive morphotype of both mesonychians and cetaceans. Here, I describe some of the first postcranial material of *Hapalodectes,* compare it with certain mesonychids, and discuss the implications of this specimen for the phylogeny of Mesonychia.

DESCRIPTION

The specimen (AMNH 17558) of *Hapalodectes* was collected in 1918 from a locality identified as "Apadock Gulch", Huerfano Formation, Colorado, a formation that has

→

Fig. 2. Right distal humeri of three mesonychians. Left column, anterior view; middle column, medial view; right column, posterior view. Top row, *Mesonyx* (AMNH 12160); middle row, *Dissacus* (AMNH 3359); bottom row, *Hapalodectes* cf. *leptognathus* (AMNH 17558). Abbreviations: **dp** deltopectoral crest; **entf** entepicondylar foramen; **me** medial epicondyle; **of** olecranon fossa; **sc** supinator crest; **stf** supratrochlear foramen. Scale = 10 mm.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been referred to the Lostcabinian subage of the early Eocene Wasatchian Land Mammal Age (Savage and Russell, 1983). The material consists of a distal humerus, distal metapodial, and a fragmentary but diagnostic lower dentition (fig. 1). The dentition preserves the talonid of the right M_3, which is laterally compressed and lacks both a hypoconulid and entoconid, a morphology that is diagnostic for mesonychians. The specimen is certainly a hapalodectid rather than another mesonychian because, as is typical of all hapalodectids except *Hapalorestes* (Gunnell and Gingerich, 1996), it is less than half the size of other mesonychians. On the basis of tooth size the specimen is referred to *Hapalodectes* cf. *leptognathus.* Direct comparison of this specimen with the only other genus of hapalodectid, *Hapalorestes,* is impossible due to the fragmentary nature of the holotype and only described specimen of *Hapalorestes.* It appears, however, that AMNH 17558 is smaller than that specimen. Identification of AMNH 17558 as *Hapalodectes* cf. *leptognathus* is also consistent with data on the temporal distribution of species of *Hapalodectes* (Zhou and Gingerich, 1991).

The humerus (fig. 2) preserves the distal half of the shaft and the distal articular surface. The deltopectoral crest, site of insertion of forearm flexors and extensors (Davis, 1964; Getty, 1975; Evans and Christensen, 1979) is incompletely preserved but appears to have been better developed and more distally extensive than in *Mesonyx* (fig. 2, medial view), approximating the condition in *Dissacus.* The deltopectoral crest is not as enlarged or distally extensive as that of the generalized quadruped *Ursus* (O'Leary and Rose, 1995b). A more proximal insertion for these muscles, such as is seen in *Mesonyx,* results in a short in-lever at this joint and is associated with a derived skeletal modification for speed. *Hapalodectes,* however, appears to have been less derived in this feature than was *Mesonyx.*

The supinator crest (supracondylar ridge), slightly broken, is somewhat reduced in comparison with a generalized terrestrial mammal like *Ursus* (O'Leary and Rose, 1995b). The relative size of the ridge resembles that of *Dissacus* and *Mesonyx.* A reduced supracondylar ridge is characteristic of cursorial mammals (O'Leary and Rose, 1995b), and each of these mesonychians appear to be relatively similar in this respect. The distal end of the humerus of *Hapalodectes* is not as wide as that of very generalized mammals such as *Chriacus* and *Ursus* (O'Leary and Rose, 1995b). The entepicondyle for attachment of the forearm flexors and the pronator teres is incompletely preserved at its posteroinferior margin but appears to have been somewhat large with a substantial entepicondylar foramen, presumably for passage of the median nerve and brachial artery. The mediolateral width of the articular surface is substantially broader than that of either *Dissacus* or *Mesonyx.* The capitulum in *Hapalodectes* is more rounded than that of *Mesonyx,* which is laterally compressed. A rounded capitulum allows for greater supinatory ability at the radio-humeral joint. This feature is reduced in more cursorial mesonychians like *Mesonyx,* in which this joint is more tightly interlocking and most likely allowed for greater stability of the joint at higher speeds. The capitulum is also slightly broader mediolaterally than in *Dissacus* or *Mesonyx,* again resembling more closely the condition in generalized terrestrial mammals (O'Leary and Rose, 1995b). The trochlea is less steeply angled inferomedially than that of either *Mesonyx* or *Dissacus* and does not extend as far inferiorly.

The olecranon fossa of *Hapalodectes* is relatively shallow and does not have a supratrochlear foramen (fig. 2). By contrast, in *Dissacus* and to a greater degree in *Mesonyx,* these fossae are deep, indicating that these mesonychians exhibited greater range of extension of the forearm than did *Hapalodectes.* The shallow olecranon fossa of *Hapalodectes* suggests that this animal habitually held its forearm in a semiflexed position (O'Leary and Rose, 1995b). Measurements are given in table 1.

DISCUSSION

These postcranial data for *Hapalodectes* suggest that it was not as cursorial as either *Dissacus* or *Mesonyx. Hapalodectes,* with its moderately well-developed deltopectoral crest, relatively wide distal articular surface, somewhat rounded capitulum, and shallow,

TABLE 1
Measurements of *Hapalodectes* Specimen (in mm)

Humerus	
Anteroposterior depth at base of deltopectoral crest	8.3 mm
Mediolateral width of articular surface	11.4
Maximum mediolateral width across epicondyles	13.4
Total length of preserved portion	44.5
Dentition	
M_2 length	5.7
M_3 length	7.3
Depth of dentary under M_2 (mesial aspect)	12.8

imperforate olecranon fossa, appears to have been terrestrial but to have lacked the cursorial specializations of other mesonychians. This specimen differs from that mentioned but not figured by Rose (1990), which has a deep olecranon fossa and other features consistent with enhanced extension of the elbow and cursoriality. The early Eocene radiation of hapalodectids appears to have been characterized by variation in postcranial morphology, something which will be best understood as other specimens are figured and described.

On the basis of current evidence the phylogenetic position of *Hapalodectes* remains unresolved (Geisler and O'Leary, 1997); this taxon sometimes clusters with a monophyletic Mesonychidae to the exclusion of Cetacea and sometimes falls outside a mesonychid–cetacean clade, making Mesonychia paraphyletic. The postcranial information described here is currently being included in a larger study of ungulate relationships (O'Leary and Geisler, in prep.). At present it is clear that cursoriality characterizes the more highly nested members of Mesonychidae (e.g., *Pachyaena* and *Mesonyx*) (Geisler and O'Leary, 1997) but not necessarily those taxa at the base of the clade, such as *Hapalodectes*. If hapalodectids form a monophyletic clade with mesonychids, the hypothesis that cursoriality was not a primitive feature of the entire mesonychian clade must be considered. This is significant because it suggests that when further evidence becomes available for direct comparison of various postcranial elements, derived features of the most primitive whale skeleton known, *Ambulocetus* (Thewissen et al., 1996), such as the relatively grooved proximal astragalus, may not be synapomorphies of Mesonychia and Cetacea but instead homoplasies. Alternative hypotheses, such as that the postcranial morphology of *Hapalodectes* represents a reversal or that Mesonychia is paraphyletic with respect to Cetacea, cannot be rejected without further data. Retrieval of other skeletal elements of *Hapalodectes,* particularly an astragalus, will be important for establishing the basal mesonychian morphotype and for understanding the relationship of this clade to Cetacea.

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